Ecology, 81(11), 2000, pp. 3237–3243

TREE-RING VARIATION IN PINYON PREDICTS LIKELIHOOD OF DEATH FOLLOWING SEVERE DROUGHT

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Abstract. A severe drought in northern Arizona caused widespread pinyon (*Pinus edulis*) mortality, exceeding 40% in some populations. We measured tree-ring widths of pinyons that survived and that died in three sites designated as ''high,'' ''medium,'' and ''low'' stress. Growth characteristics during the previous 10–15 years can be used to predict the likelihood of drought-induced death; dead trees exhibited 1.5 times greater variation in growth than live trees. A model of ring-width deviations vs. drought severity showed a loss of ''climatic sensitivity'' with age in dead trees. These differences were independent of site. We found two distinct tree types that are predisposed to die during drought; highly sensitive young trees, and insensitive older trees. As the Southwest has a dynamic climate typified by severe droughts, it is important to understand how droughts act as bottleneck events to affect a dominant tree in a major vegetation type of the United States.

Key words: climatic sensitivity; drought; environmental stress; mortality, likelihood following drought; Pinus edulis; *pinyon pine; tree rings.*

Introduction

General circulation models project that a doubling of atmospheric CO_2 in the near future will result in shifts in the spatio-temporal distribution of precipitation (e.g., Cubasch et al. 1995). Complex interactions between the terrestrial biosphere and a changing climate are predicted to dramatically affect vegetation responses (Neilson and Drapek 1998). By studying current patterns of drought-induced plant death, we may be able to predict important population and community-level responses to various climate change scenarios.

Severe droughts have the potential to greatly impact pinyon (*Pinus edulis*) populations and their associated communities. In northern Arizona, a severe drought in 1996 resulted in high pinyon mortality rates, exceeding 40% on south-facing slopes of cinder cones where the effects of drought are likely to be most severe. Pinyon is an appropriate tree for study because it is considered to be drought adapted, and it is widely distributed across Mexico and the western United States (Mirov 1967, Lanner and Van Devender 1998). Moreover, a rich history of its biogeographical expansion with the changing climate of the last 40 000 yr has accumulated (Betancourt 1987, Betancourt et al. 1990), allowing us to place current changes into a paleoecological perspective. From a community perspective, much is known about how environmental stress affects pinyons, which in turn affects insect herbivores (Mopper et al. 1991, Cobb et al. 1997), mycorrhizal mutualists (Gehring and Whitham 1994, Gehring et al. 1998), birds and mammals (Christensen and Whitham 1991, 1993).

The purpose of this study was to compare growth attributes of pinyons that died (''dead'') during the 1996 drought with those that survived (''live''). We hypothesized that, prior to death, dead pinyons were more sensitive than live trees to wet and dry events, and this greater sensitivity should be expressed as greater ring-width variation. Though variance in ring widths has been adopted as an index of environmental sensitivity (e.g., Fritts 1974, 1976), it does not separate the components of the tree's environment that drive the response (e.g., climate, herbivory, nutrients, competition). We focused on the role of climate by modeling ring-width responses to drought severity and tested for differences in ''climatic sensitivity'' between live and dead trees. This analysis allowed us to investigate how climatic sensitivity varies across the extreme water and nutrient-stressed cinder soils of Sunset Crater National Monument (35°22′ N, 111°32′ W) and adjacent sandy loam soils (e.g., Table 1).

This study is unique in several aspects: (1) very high pinyon mortality during 1996 provided large sample sizes; (2) we are unaware of any study that has ex-

Manuscript received 24 May 1999; revised 10 January 2000; accepted 13 January 2000; final version received 4 February 2000.

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TABLE 1. Site characteristics of cinder and sandy-loam sites and pinyon pine performance that reflect differences in degree of environmental stress.

Parameter†	Cinder soils‡	Sandy loam soils
Mean air temperature (°C)	20.3	20.8
Mean daily precipitation (mm)	1.56	1.66
Gravimetric soil water content (%)	3.2	5.6*
Mean soil temperature (°C)	17.2	13.8*
Extractable phosphate (μg/g)	4.45	12.20*
Soil NO_3 mineralization ($\mu g \cdot g^{-1} \cdot d^{-1}$)	0.015	0.147*
Soil NH_4 mineralization ($\mu g \cdot g^{-1} \cdot d^{-1}$)	−0.012	0.062*
Mean number of female cones per tree	185.0	300.0*
Mean xylem pressure (MPa)		
Mean stem growth (length, mm)	−2.83	−2.38*
	33.36	46.32

* Significant site effect ($P \leq 0.005$).

† Obtained from Christensen and Whitham (1991), Mopper et al. (1991), Gehring and Whitham (1994), Cobb et al. (1997), and Swaty et al. (1998).

‡ Data only available for flat terrain; south-facing slopes of cinder cones were not investigated.

amined variability in growth as a predictor of drought-induced mortality; and (3) we sampled pinyons across a wide range of ages to tease apart interactions between age, sensitivity to climate, and drought tolerance. We address this question: ‘‘Can we use patterns of tree-ring variation to predict who will live and die during a severe drought?’’ Understanding how severe droughts might act as bottleneck events and affect selection pressures is important for generating predictions of the potential impact of climate change on gene frequencies, species composition, and ecosystem function.

METHODS

Sites, mortality transects, and tree cores

Trees were growing in three habitat types in the Coconino National Forest in northern Arizona. Habitat types were operationally defined as ‘‘high,’’ ‘‘medium,’’ and ‘‘low’’ stress based on slope, aspect, and soil type. South-facing slopes of cinder cones within Sunset Crater National Monument characterize the high stress habitat; the medium stress site consisted of cinder soil flat terrain and occurred in this same area. The low stress habitat was characterized by sandy loam soil ∼10–15 km to the south of the cinder soil sites. Our justification for these three stress classifications is based on previous studies at these same sites (Table 1).

From fall 1996 to spring 1997 we counted numbers of dead and live pinyon encountered in 40–50 m wide transects (∼15 each in the low and medium stress sites). Transects were conducted away from roads, were 2–4 km long, and ranged in elevation from 1740–2120 m. For the high stress site, we sampled transects parallel to the slope of southern exposed faces of seven cinder cones for a total of 21 transects. Length and number of transects per cone varied depending on cone size. We pooled transect data within each habitat to estimate site-specific mortality.

We collected tree cores to quantify growth; dead and live pinyons (diameter ≥ 8 cm) were paired by size and proximity (5–50 m apart) to reduce variation in growth due to differences in age, competition, and microsite. Due to logistics, we were limited to collecting one core from each bole, as near to the base as possible for accurate aging; additional cores were collected if the first core was damaged or greatly missed the pith. Trees on slopes were bored parallel to the slope to avoid reaction and tension wood so that growth was not over or under estimated. We followed methods of Swetnam et al. (1988) for preparing cores. Cross dating was accomplished by visually comparing skeleton plots with master chronologies for nearby sites, downloaded from the International Tree Ring Data Bank (ITRDB).[2] For recent years, we used 1989 as a marker year because it was characterized by a relatively severe drought and resulted in narrow rings.

Tree growth, climatic sensitivity, age, and drought tolerance

We began by examining simple growth characteristics of dead and live pinyon across the three different sites. These included lifetime growth rate (mean ring width), recent (1986–1995) growth rate, and variance in mean lifetime ring-width index. Ring-width indices were calculated to remove the inherent effect of tree age on growth. For each series, we modeled the age trend in the raw widths by fitting linear and negative exponential functions to the data, and selected the appropriate model by comparing correlation coefficients and residuals. Indices were obtained by dividing the raw widths for each series by the predicted width given by the model fit. Growth attributes of dead and live pinyon were compared in an ANOVA with site and mortality class as fixed factors, and dead and live trees were blocked by pair number (random factor) (SAS 1990; mixed models procedure).

Our main objective was to model ring-width variation as a function of age, climate, and habitat type to investigate how climatic sensitivity differed between dead and live pinyon growing along an environmental stress gradient. We modeled growth as a function of Palmer Drought Severity Indices (PDSIs, based on precipitation, evapotranspiration, soil properties, and accumulated effects of past conditions on present weath-

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[2] NOAA Paleoclimatology Program, Boulder, Colorado, USA. URL: ⟨http://www.ngdc.noaa.gov/paleo/⟩.

er; see Palmer 1965); analyses showed that ring widths were better correlated with PDSI than with rainfall (also see Cook and Jacoby 1977, Nichols 1989, Jenkins and Pallardy 1995). We used growing season (May–October) PDSI because analyses showed that ring widths were better correlated with growing season than with annual or other seasonal PDSIs. We downloaded PDSIs from the National Climatic Data Center (NCDC).[3] Our study area bordered National Oceanic and Atmospheric Administration (NOAA) designated Arizona Climatic Divisions 2, 3, and 4 (mostly delineated by topographic boundaries); thus, we pooled PDSIs across these regions to describe average drought severity patterns.

We calculated ring-width deviations for each tree from 1980–1995 by subtracting each tree's 1980–1995 mean ring width from each annual width. Ring-width deviation (y) was modeled in a repeated-measures ANCOVA (rANCOVA), with site and mortality as fixed factors and mean growing season PDSI and tree age at time of study as covariates (SAS 1990; mixed models procedure). The covariance structure was modeled as first-order autoregressive (i.e., AR[1]) to account for correlated errors, which is commonly observed in ring widths (Fritts 1974, Cook and Jacoby 1977, Pedersen 1998). Covariance parameters were estimated separately for each site. Growth of dead and live trees was modeled as: $y = b_0 + b_1 \times \text{age} + b_2 \times \text{PDSI} + b_3 \times \text{age} \times \text{PDSI} = b_0 + b_1 \times \text{age} + (b_2 + b_3 \times \text{age}) \times \text{PDSI}$. Contrasts were constructed to test for differences in sensitivity to climatic variation between dead and live trees; an index of this sensitivity is given by $b_2 + b_3 \times \text{age}$ (a larger value implies greater sensitivity). Because this response depends on age, tests were conducted for five ages (40, 80, 120, 160, and 200 yr) that spanned the range sampled in this study. Each model was tested for a significant age × PDSI interaction to determine if climatic sensitivity changes with age, and if the effect of age depends on the ability of a tree to withstand drought.

We recognize that using ring-width deviations may yield potential problems; e.g., widths generally decrease with age, and thus the deviations are expected to be smaller for older trees. An alternative is to use ratios (or indices); hence, we also calculated indices for each tree from 1980–1995 by dividing each annual width by the tree's 1980–1995 mean width. However, ring-width indices are also associated with potential problems; below average growth is bounded between zero and one and above average growth is only bounded below by one (also see Cook and Peters 1997). For comparison, we also conducted an rANCOVA with ring-width indices.

RESULTS

Pinyon growth and mortality across an edaphic stress gradient

Pinyon lifetime growth rates and ring-width variability varied predictably across the designated stress gradient. Growth was lowest for trees growing on south-facing slopes of cinder cones and highest for those in sandy loam soils (Table 2). Trees growing on south-facing slopes of cinder cones also exhibited 85% greater variation in growth than trees in sandy loam soils (Table 2). We rejected the alternative hypothesis that these differences could be due to dissimilar tree ages because age did not differ between sites (Table 2).

Pinyon mortality across the edaphic stress gradient indicated a positive relationship between stress and mortality (Table 2). Mortality rates on south-facing cinder slopes were 6× greater than on flat terrain cinders, and 2.5× greater than on sandy loam soils. However, the pattern was opposite of what we predicted for the latter two sites; mortality rates in cinder soils of reduced exposure were significantly lower than in the sandy loam soil (z test, $P \leq 0.0001$).

Although we found differences between pinyon populations growing in the three distinct habitats; differences in mean ring width and ring-width variability of dead vs. live pinyons did not change with soil type or exposure. Thus, we compared dead and live trees pooled across sites. In support of our hypothesis, dead pinyons showed significantly greater variation in lifetime ring-width indices; however, this difference was solely due to dissimilar recent (1986–1995) variances (Table 2). Excluding the year of death, trees that died in 1996 did not differ in their mean lifetime growth rates from survivors; but, recent growth rates were significantly reduced in dead relative to live trees (Table 2). Paired dead and live trees did not differ in age; thus, these differences in recent growth patterns could not be due to different tree ages (Table 2).

Integrating climatic sensitivity, age, and stress

Recent growth patterns appear to be very important to determining which trees live and die during a drought. To further investigate recent growth characteristics, we modeled ring-width variability from 1980–1995 as a function of mortality class, climate, tree age, and habitat type. We found distinct differences between dead and live pinyon that were constant across the three habitats (rANCOVA, site and all site interactions, $P \geq 0.5361$). Because of these consistencies, trees were pooled across sites.

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[3] NOAA, Asheville, North Carolina, USA. URL: ⟨http://www.ncdc.noaa.gov/⟩

TABLE 2. Pinyon pine performance that reflects differences in degree of environmental stress and ability to survive drought.

Parameter	Cinder soils (south-facing slopes)†	Cinder soils (flat terrain)	Sandy loam soils
Mortality rate (%)†	13.5 ± 0.59 (3396)^{A}	2.3 ± 0.17 (8136)^{B}	5.4 ± 0.26 (7484)^{C}
Lifetime growth rate (mm/yr)‡	0.93 ± 0.040 (78)^{A,B}	1.05 ± 0.066 (36)^{A}	1.09 ± 0.068 (44)^{B}
Variance in mean lifetime index	0.22 ± 0.023 (40)^{A}	0.19 ± 0.019 (24)^{B}	0.12 ± 0.010 (26)^{A}
Recent 10-yr growth rate (mm/yr)	1.13 ± 0.099 (40)^{A}	1.03 ± 0.094 (24)^{A}	0.95 ± 0.086 (26)^{A}
Tree age of sampled trees (yr)	103.5 ± 8.03 (78)^{A}	97.7 ± 3.03 (36)^{A}	87.1 ± 8.13 (44)^{A}

Parameter	Dead pinyon§	Live pinyon
Lifetime growth rate (mm/yr)‡	0.98 ± 0.036 (80)	1.00 ± 0.034 (78)
Variance in mean lifetime ring-width index	0.23 ± 0.018 (45)	0.18 ± 0.015 (45)*
Recent 10-yr growth rate (mm/yr)	0.85 ± 0.053 (45)	1.07 ± 0.062 (45)*
Tree age of sampled trees (yr)	96.7 ± 4.73 (80)	97.9 ± 5.56 (78)
Variance in mean ring-width index prior to 1980	0.18 ± 0.016 (45)	0.17 ± 0.017 (45)
Variance in mean 1980–1995 ring-width index	0.29 ± 0.051 (45)	0.20 ± 0.028 (45)*

Note Table entries are means ± 1SE (*n*). Different letters within a row in the top panel indicate significant pairwise differences ($P \leq 0.05$).

* Significant mortality effect ($P \leq 0.05$).

† Samples size (*n*) represents the total number of trees censused (i.e., dead + live).

‡ Basal diameter divided by number of rings; if there was no pith, we estimated the number of missing rings.

§ Means for dead and live trees are pooled across sites. Because of the lack of a mortality × site interaction, we do not show means for dead and live trees within sites.

The most striking difference between dead and live pinyons is the effect of tree age on climatic sensitivity; e.g., in Fig. 1, climatic sensitivity is reflected in the distance between contour lines (predicted ring-width deviations). In live trees, the age × PDSI interaction was nonsignificant (rANCOVA contrast, $t_{1299} = -0.62$, $P = 0.5349$) and the relatively flat, parallel, and evenly spaced contours in Fig. 1A suggest that all trees responded similarly to changes in PDSI. For each unit change in PDSI, ring widths of trees from all ages are predicted to change by ~0.1 mm.

Pinyons that died during the 1996 drought exhibited a very different pattern. A significant age × PDSI interaction (rANCOVA contrast, $t_{1299} = -4.70$, $P \leq 0.0001$) and the divergent, nonlinear, and unevenly spaced contours in Fig. 1B show that response to changes in PDSI depends on age. The closely spaced contours for 40-yr-old trees suggest that young trees are highly sensitive to climatic variation; for a unit change in PDSI, a ''large'' change (~0.15 mm) in ring widths is predicted. This response diminishes as trees age such that changes in PDSI are barely reflected in the rings of old (150–200 yr) trees.

We initially hypothesized that dead pinyons were more sensitive to climatic variation than neighboring live trees; however, as this sensitivity depends on tree age, our hypothesis is only supported for young trees. For example, a 40-yr-old tree that died during the 1996 drought was ~1.2× more sensitive than a live tree of similar age ($b_2 + b_3 \times \text{age} = 0.122$ and 0.099 for dead and live trees, respectively). Dead trees become less sensitive than live trees with increasing age; a 200-yr-old live tree was ~12.6× more sensitive than a 200-yr-old dead tree ($b_2 + b_3 \times \text{age} = 0.007$ and 0.086 for dead and live trees, respectively). The ''critical age'' at which dead trees became less sensitive than live trees is 60–80 yr.

Similar results were found for ring-width indices; a significant age × PDSI existed for dead trees (but not for live trees) such that the effect of tree age reduces this sensitivity (Fig. 1C, D). Although the age × PDSI interaction is not as pronounced for indices, young dead trees were still more sensitive than young live ones, and the critical age shifted to ~100–120 yr.

DISCUSSION

Record droughts as bottleneck events

Although droughts of similar magnitude to the 1996 drought are uncommon, they can have devastating effects on plant and animal populations. The 1996 drought in northern Arizona caused pinyon populations to suffer unusually high mortality, surpassing 40% local mortality in the present study and reaching 80% in another study (T. Whitham, *unpublished data*). Likewise, Betancourt et al. (1993) found widespread pinyon mortality in response to the 1950–1956 drought in New Mexico. Such high mortality could result in bottleneck events that reduce genetic variation or favor drought-adapted genotypes.

Rare droughts can also alter community structure and function. For example, a classical symptom of land degradation in arid lands (''desertification'') is a transition from grasslands to shrublands (Schlesinger et al. 1990). Swetnam and Betancourt (1998) showed that the record mid-1950s New Mexico drought resulted in

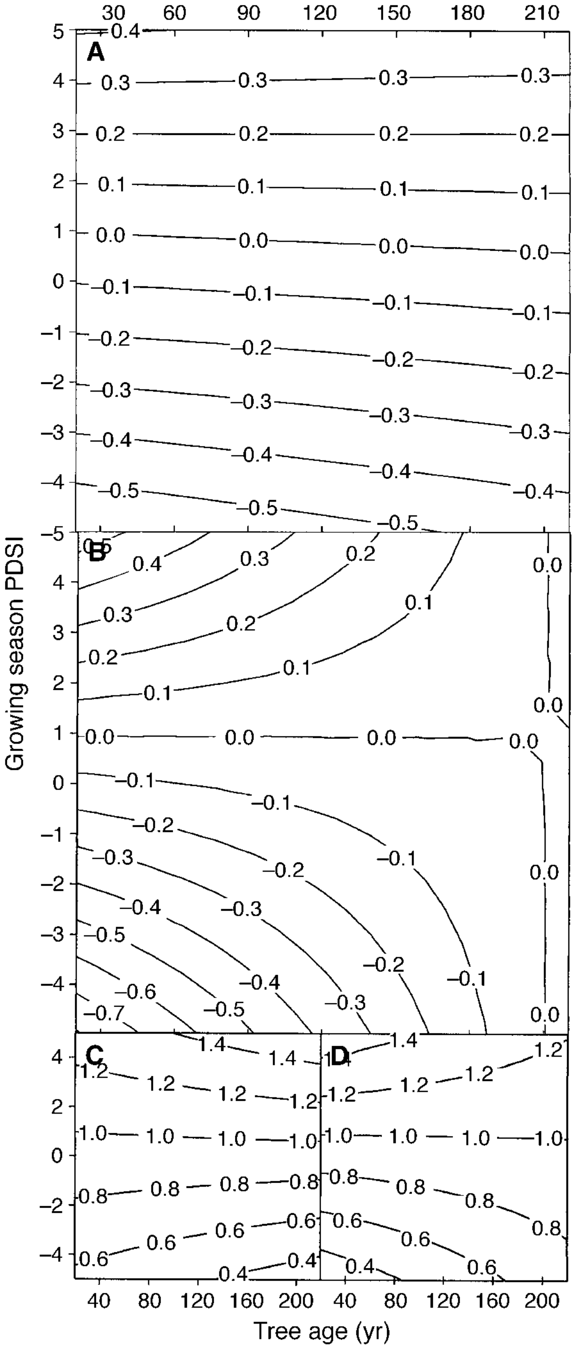

FIG. 1. Predicted ring-width deviations and indices of dead and live pinyons were pooled across sites, as site and all its interactions were nonsignificant ($P > 0.05$). In (A) and (B), contour lines are predicted ring-width deviations (mm) of dead and live pinyon as a function of growing season (May–October) PDSI and tree age. (A) Live pinyons: $y = -0.105 + 0.284 \times 10^{-3} \times$ age $+ 0.103 \times$ PDSI $- 0.087 \times 10^{-3} \times$ age $\times$ PDSI. Relatively flat, parallel, and evenly spaced contours suggest that trees of all ages respond similarly to climatic variation.

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(B) Dead pinyons: $y = -0.139 + 0.663 \times 10^{-3} \times$ age $+ 0.151 \times$ PDSI $- 0.721 \times 10^{-3} \times$ age $\times$ PDSI.Divergent, curved, and unevenly spaced contours show that response to climatic variation is age dependent. The closely spaced contours for trees ~40 yr old suggest that ring widths are highly sensitive to PDSI.

In (C) and (D), contour lines are predicted ring-width indices (ratios). (C) A similar response is shown when using ring-width indices vs. ring-width deviations; predicted indices are relatively flat for live trees, although there is some indication that sensitivity increases with age (i.e., contour lines become closer, but this is not a significant trend, $P = 0.09$). (D) A similar response is also shown for predicted ring-width indices vs. predicted ring-width deviations of dead trees, but the effect of tree age is not as pronounced. Similar to deviation predictions, older trees exhibited reduced sensitivity when compared to younger trees.

widespread plant mortality and accelerated the invasion of shrubs into grasslands. Given the potential of climate change, the role of drought in shaping communities and affecting selection pressures in these systems will likely become even more important (see also Allen and Breshears 1998).

Pinyon growth patterns confirm stress gradient

Our designation of “low”, “medium”, and “high” stress habitats was supported by pinyon lifetime growth patterns (Table 2). Greater tree-ring variation is associated with greater environmental stress (also see Fritts et al. 1965, Fritts 1976). Greater environmental stress is also associated with greater asymmetry in birch leaves (Wilsey et al. 1998) and deer antlers (Pélabon and van Breukelen 1998). Greater ring-width variability and lower growth rates in cinder soils vs. sandy loam soils are consistent with other studies indicating that the cinder soils are more stressful (Table 1).

Based on these observations, we hypothesized that drought-induced pinyon mortality would decrease across the cinder soil to sandy loam continuum. Although these predictions held across soil extremes, the medium stress site suffered lower mortality than expected (Table 2). Two hypotheses may account for this result. First, preconditioning of pinyon growing in the cinder soil “flats” may have made them less likely to die during the drought than trees in sandy loam soils; in the laboratory, plants receiving pretreatments of mild to moderate drought exhibited improved water relations and greater survival than controls during subsequent water stress (Zwiazek and Blake 1989, Cregg 1994). Second, local variation in monsoonal precipitation could have “converted” the low stress site to a medium stress site in 1996. Total precipitation during 1995–1996 recorded at two weather stations nearest to the cinder soil sites was 61% and 85% of their respective 1970–1994 means. However, at a third weather station, nearest to the sandy loam sites, precipitation was a mere 37% of the 1970–1994 mean, which shows that the severity of the 1996 drought was likely not constant across our study sites.

Integrating growth, climatic sensitivity, age, and stress

Patterns of lifetime growth strongly argue that variation in growth is just as important as mean growth to predicting survival because it reflects the degree to which organisms respond to short-term abiotic uncertainties. Deviation from the mean phenotype has been associated with fecundity and mortality in both plants and animals (e.g., Hunt and Allen 1998, Pélabon and van Breukelen 1998). In the present study, greater tree-ring variation is strongly and positively correlated with drought-induced mortality and may be used as an index of drought tolerance.

Although studies to date emphasize declining vigor as a prominent characteristic of dying trees (e.g., Jenkins and Pallardy 1995, Pedersen 1998), we show that variation in growth may play a more important role. For example, if two pinyons of similar age are growing side by side, then 72% of the time we will accurately predict that the tree with recent reduced growth is more likely to die during a drought (1986–1995 mean ring widths were smaller for dead vs. live trees in 31 of 43 pairs). Likewise, a prediction that the tree with greater recent ring-width variability is more likely to die will be correct 72% of the time. Additionally, if the two trees are younger than the critical age of 70 yr, then we will correctly predict 61% of the time that the tree with heightened climatic sensitivity is more likely to die. If the trees are older than 70 yr, then we will correctly predict 80% of the time that the one with reduced sensitivity is more likely to die. Furthermore, if all three criteria are assessed, then our confidence in our predictions increases to 85% (i.e., dead trees exhibited at least two of three of these characteristics in 28 of 33 pairs for which growth, ring-width variability, and climatic sensitivity were assessed).

Mechanisms

We propose three major mechanisms that likely influence which trees live or die during severe droughts. These mechanisms are highly coupled and are likely to operate at different temporal scales. For example, the genetic composition of dead and live pinyon was probably very important and there is evidence that drought tolerance within the cinder soils is linked to the glycerate dehydrogenase locus (Cobb et al. 1994). Second, biomass allocation patterns may have differed; e.g., live trees may have allocated more biomass to roots (e.g., Cregg 1994) relative to shoots, such that they were less limited by soil water. Third, drought-induced death could be attributed to a variety of physiological processes (Mitton 1995) that could be linked to genetics and/or biomass allocation patterns.

ACKNOWLEDGMENTS

We thank H. Grissino-Mayer for his constructive comments, and J. Betancourt, T. Swetnam, R. Adams, and others from the Laboratory of Tree-Ring Research, University of Arizona at Tucson, for valuable assistance in techniques. We thank T. Grout, J. Schively, E. Stanley, and J. Ruel for field and laboratory assistance, and J. Barber for statistical advice. We also thank the ITRDB, D. Graybill, and J. Dean for making available the master chronologies, and the personnel from the Coconino National Forest for their cooperation. We acknowledge the DRI and the Wesclim database (http://www.wrcc.sage.dri.edu/) for precipitation data. This research was funded by NSF grants LTREB9615313 and DEB-9726648, and USDA grant 97-35302-4241.1.

LITERATURE CITED

Allen, C. D., and D. D. Breshears. 1998. Drought-induced shift of a forest–woodland ecotone: rapid landscape response to climate variation. Proceedings National Academy Sciences USA **95**:14839–14842.

Betancourt, J. L. 1987. Paleoecology of pinyon-juniper woodlands: summary. Proceedings of the Pinyon-Juniper Conference. General Technical Report, Reno, Nevada. USDA Forest Service, Intermountain Research Station **215**: 129–140.

Betancourt, J. L., P. S. Martin, and T. R. Van Devender. 1990. Packrat middens: the last 40,000 years of biotic change. University of Arizona Press, Tucson, Arizona, USA.

Betancourt, J. L., E. A. Pierson, K. A. Rylander, J. A. Fairchild-Parks, and J. S. Dean. 1993. Influence of history and climate on New Mexico piñon-juniper woodlands. Pages 42–62 *in* E. F. Aldon, and D. W. Shaw, editors. Managing piñon-juniper ecosystems for sustainability and social needs. USDA Forest Service Technical Report RM-236.

Christensen, K. M., and T. G. Whitham. 1991. Indirect herbivore mediation of avian seed dispersal in pinyon pine. Ecology **72**:534–542.

Christensen, K. M., and T. G. Whitham. 1993. Herbivore impact on competition between birds and mammals for pinyon pine seeds. Ecology **74**:2270–2278.

Cobb, N. S., J. B. Mitton, and T. G. Whitham. 1994. Genetic variation associated with chronic water and nutrient stress in pinyon pine. American Journal of Botany **81**:936–940.

Cobb, N. S., S. Mopper, C. A. Gehring, M. Caouette, K. M. Christensen, and T. G. Whitham. 1997. Increased moth herbivory associated with environmental stress of pinyon pine at local and regional levels. Oecologia **109**:389–397.

Cook, E. R., and G. C. Jacoby, Jr. 1977. Tree-ring–drought relationships in the Hudson Valley, New York. Science **198**: 399–401.

Cook, E. R., and K. Peters. 1997. Calculating unbiased tree-ring indices for the study of climatic and environmental change. Holocene **7**:361–370.

Cregg, B. M. 1994. Carbon allocation, gas exchange, and needle morphology of *Pinus ponderosa* genotypes known to differ in growth and survival under imposed drought. Tree Physiology **14**:883–898.

Cubasch, U., J. Waszkewitz, G. Hegerl, and J. Perlwitz. 1995. Regional climate changes as simulated in time-slice experiments. Climate Change **31**:273–304.

Fritts, H. C. 1974. Relationships of ring widths in arid-site conifers to variations in monthly temperature and precipitation. Ecological Monographs **44**:411–440.

Fritts, H. C. 1976. Tree rings and climate. Academic Press, New York, New York, USA.

Fritts, H. C., D. G. Smith, J. W. Cardis, and C. A. Budelsky. 1965. Tree-ring characteristics along a vegetation gradient in northern Arizona. Ecology **46**:393–401.

Gehring, C. A., T. C. Theimer, T. G. Whitham, and P. Keim. 1998. Ectomycorrhizal fungal community structure of pinyon pines growing in two environmental extremes. Ecology **79**:1562–1572.

Gehring, C. A., and T. G. Whitham. 1994. Comparisons of ectomycorrhizae on pinyon pine (*Pinus edulis*; Pinaceae) across extremes of soil type and herbivory. American Journal of Botany **81**:1509–1516.

Hunt, J., and G. R. Allen. 1998. Fluctuating asymmetry, cell structure and the risk of attack from phonotactic parasitoids in the bushcricket *Sciarasaga quadrata* (Orthoptera: Tettigoniidae). Oecologia **116**:356–364.

Jenkins, M. A., and S. G. Pallardy. 1995. The influence of drought on red oak group species growth and mortality in the Missouri Ozarks. Canadian Journal of Forest Research **25**:1119–1127.

Lanner, R. M., and T. R. Van Devender. 1998. The recent history of pinyon pines in the American Southwest. Pages 171–182 *in* D. M. Richardson, editor. Ecology and biogeography of *Pinus.* Cambridge University Press, Cambridge, UK.

Mirov, N. T. 1967. The genus *Pinus*. Ronald Press, New York, USA.

Mitton, J. B. 1995. Genetics and the physiological ecology of conifers. Pages 1–36 *in* W. K. Smith, and T. M. Hinckley, editors. Ecophysiology of coniferous forests. Academic Press, San Diego, California, USA.

Mopper, S., J. B. Mitton, T. G. Whitham, N. S. Cobb, and K. M. Christensen. 1991. Genetic differentiation and heterozygosity in pinyon pine associated with resistance to herbivory and environmental stress. Evolution **45**:989–999.

Neilson, R. P., and R. J. Drapek. 1998. Potentially complex biosphere responses to transient global warming. Global Change Biology **4**:505–521.

Nichols, W. D. 1989. Reconstructed drought history, north-central Great Basin. Pages 1601–1982 *in* D. H. Peterson, editor. Aspects of climatic variability in the Pacific and the western Americas.Geophysical Monograph **55**:61–67.

Palmer, W. C. 1965. Meteorological drought. Research Paper No. 45. U.S. Department of Commerce, Weather Bureau, Washington, D.C., USA.

Pedersen, B. S. 1998. The role of stress in the mortality of Midwestern oaks as indicated by growth prior to death. Ecology **79**:79–93.

Pélabon, C., and L. van Breukelen. 1998. Asymmetry in antler size in roe deer (*Capreolus capreolus*): an index of individual and population conditions. Oecologia **116**:1–8.

SAS 1990. SAS/STAT User's Guide. Version 6. SAS Institute Cary, North Carolina, USA.

Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. Science **247**:1043–1048.

Swaty, R. L., C. A. Gehring, M. Van Ert, T. C. Theimer, P. Keim, and T. G. Whitham. 1998. Temporal variation in temperature and rainfall differentially affects ectomycorrhizal colonization at two contrasting sites. New Phytologist **139**:733–739.

Swetnam, T. W., and J. L. Betancourt. 1998. Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. Journal of Climate **11**: 3128–3147.

Swetnam, T. W., M. A. Thompson, and E. K. Sutherland. 1988. Using dendrochronology to measure radial growth of defoliated trees. USDA, Forest Service, Agricultural Handbook No. 639.

Wilsey, B. J., E. Haukioja, J. Koricheva, and M. Sulkinoja. 1998. Leaf fluctuating asymmetry increases with hybridization and elevation in tree-line birches. Ecology **79**:2092–2099.

Zwiazek, J. J., and T. J. Blake. 1989. Effects of preconditioning on subsequent water relations, stomatal sensitivity, and photosynthesis in osmotically stressed black spruce. Canadian Journal of Forest Research **67**:2240–2244.